SUPPLEMENTARY NOTES ON THE FAMILY ANATIDAE

BY JEAN DELACOUR AND ERNST MAYR

SINCE the appearance of our paper, "The Family Anatidae" (1945, *Wilson Bulletin,* 57:3–55), a few contributions to the subject have come to our knowledge, and some new facts have been reported. We think it worth while to mention them briefly.

To start with, certain of our statements might be modified as follows:

Some mergansers carry their chicks on the back, as do the Mute and Black-necked Swans (p. 9).

A few river ducks (Anatini) have no metallic colors on the speculum. Such is the case in *Anas strepera, A. angustirostris,* and in the aberrant forms: *Hymenolaimus malacorhynchos, Malacorhynchus membranaceus, Rhodonessa caryophyllacea,* and *Stictonetta naevosa* (p. 16).

The downy young of *Heteronetta atricapilla* is known, although so far undescribed (p. 54). We have examined two specimens: one is a mounted chick, lent by Herbert Friedmann, U. S. National Museum, Washington, which served as the model in the preparation of Figure 1. It was collected at Batuco Lake, 50 kilometers north of Santiago, Chile. The egg was found on September 23, 1938, in a nest of a Red-gartered Coot (*Fulica armillata*). The egg hatched on October 16, and the bird died five days later. The second is a skin lent by Josselyn Van Tyne, University of Michigan Museum of Zoology (No. 93120, ♀, 195–200 kilometers west of Puerto Casado, Paraguay, March 1, 1937, Schulze and Lopez). The accompanying figure by Alexander Seidel depicts accurately the very peculiar color pattern of this species. Unfortunately, the pattern gives no clue to the relationships of *Heteronetta.* Unique features of the duckling of this species are: unusual length of the yellowish tips of the dark down on the hind neck and upper back, and the speckled pattern on the yellow of the back, sides, and wings, produced by some long black tips. The general effect is that of a hairy and shaggy chick. The dark areas of the plumage are brown, becoming blackish-brown on the lower back, flanks, and tail. The supercilium is tawny; the sides of the head and throat are also tawny but a little darker. The breast is brownish-yellow, with a darker collar separating upper and lower throat; the abdomen paler. The markings on the wings and sides, as well as the lines on the back, are yellow. The Puerto Casado specimen is somewhat distorted by the make-up of the skin. It seems to differ from the Batuco Lake specimen in the following points: The lower abdomen and the flanks are heavily mottled with black. The superciliary stripes seem to be almost connected across the hindneck, though less pronouncedly so than in *Dendrocygna.* The longitudinal

stripes on the back seem to turn toward the flanks at their posterior ends. It remains to be seen whether any of these characters is typical for the species.

About the habits of the Bronze-winged Duck, *Anas specularis* (p. 18) Lord William Percy (*in litt.*) says:

"I lived with them for a month on a river at sea level in south Chile and, except for the similarity in the plumage pattern of the wings to that of the Crested Duck (*specularioides*), they always struck me as typical river ducks with nothing else reminiscent of a Crested Duck in their manner and habits. As to their voice there should be no doubt about that, for it is the most remarkable of any duck I know. The female's bark is as perfect an imitation of that of a small lap dog as any bird could make and I frequently mistook their note for that of dogs in the distance. I was never quite sure whether the males bark too, but they certainly have a distinctive note of their own—a single

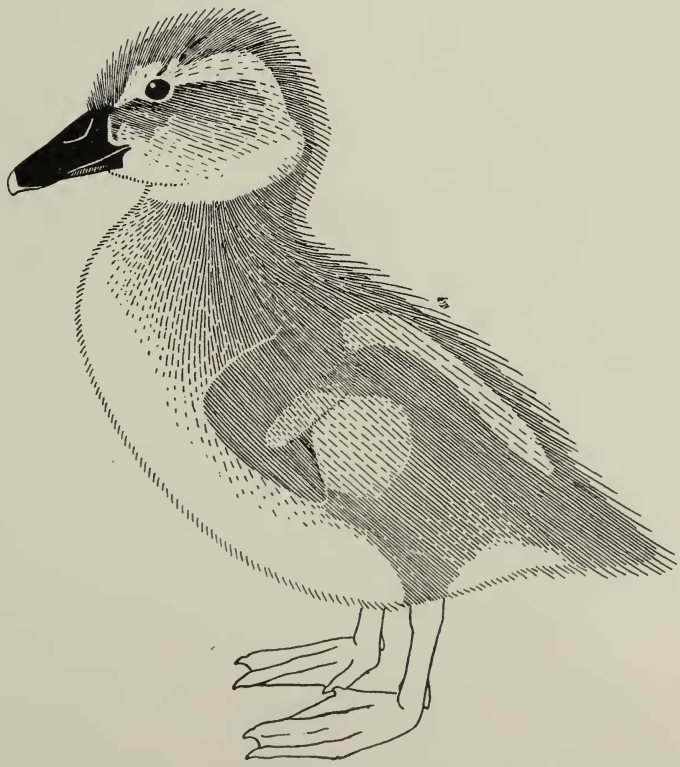

Figure 1. Black-headed Duck (*Heteronetta atricapilla*). Drawn by Alexander Seidel.

whistling note frequently repeated, but they either remain silent when the females are barking or bark too, because I never heard the whistle and barking at the same time."

Dr. John Berry, Edinburgh, Scotland, reports (*in litt.*) a case of fertility between a hybrid male *Anser anser* × *Branta bernicla* and a female of *Branta bernicla:*

"I consider that the fertility of one hybrid male of this cross was established when a Barnacle female to which he was mated, produced a gosling at Tayfield in 1944. Of course, one cannot absolutely rule out the possibility that the Barnacle mate, being full-winged, had paired with a Greylag gander. But so far as our observation went this did not occur, and all the observations pointed to the Barnacle's fertile egg having resulted from union with the hybrid gander. I was able to compare the one resulting gosling which I reared with direct hybrid goslings resulting from a Greylag × Barnacle cross. While this gosling was quite definitely not a pure Barnacle, it resembled that species much more closely than did the 'half and half' hybrids. This year the same pair of birds nested again but no eggs were hatched. At least one, however, was certainly fertile as the gosling was well formed in the egg."

Dr. Berry also rightly points out that in the Anserini, the voice of the male is usually shriller and more metallic than that of the female, which is lower, weaker, and not of a higher pitch as stated by us. He says:

"My own observations are restricted to comparatively few species, but so far as most of the true geese are concerned, I should have said the opposite. For example, in the Pink-footed Goose [*Anser fabalis brachyrhynchus*], the call note of the male is a shrill "wink wink," while that of the female is much lower. In the 'talking voice' the difference is equally marked, that of the gander being higher pitched, more nasal and metallic than the low 'muttering' of the female. The talking voice of the Bean Goose [*Anser f. fabalis*] shows a similar distinction between the lower muttering of the female and the higher more nasal voice of the ganders. The call notes of Greylag [*Anser anser*] are more or less similar, but the 'talking voice' of the female is again lower than that of the male, so too, with my White-fronted Geese [*Anser albifrons*]. I think the Snow Geese [*Anser caerulescens*] can also be sexed by the lower talking voice of the females. There may be wide variation between individuals of the same species in this matter of voice. The number of geese is small on which I have been able to determine sex beyond question by breeding or dissection, and on which I have previous precise notes of voice (confirmed by numbered rings on both legs). But in each such case I should have said, without a doubt, that the talking voice, at least, of the female was lower than that of the male."

Mr. C. L. Sibley, Wallingford, Connecticut, also reports an interesting secondary hybrid:

"You may be interested to know that this season I hatched three young from five eggs laid by a female which was herself a hybrid between a male Blue-winged Goose (*Cyanochen cyanopterus*) and a female Egyptian Goose (*Alopochen aegyptiacus*). This hybrid female mated with a Blue-winged gander which was her half-brother, and whether it was this close relationship, or inherent weakness of the three-quarters blood Blue-wing young, I lost all three.

"I had supposed that a hybrid of *Cyanochen* and *Alopochen* would be sterile, yet she laid normal-shelled eggs and hatched three. All five eggs were fertile."

New observations of the display of the Maned Goose (*Chenonetta jubata*) have been made and reported by Delacour (1945, *Wilson Bulletin,* 57:129). They confirm the relationship of this species with the Mandarin and Wood Ducks (*Aix*).

In 1941, Finn Salomonsen published a detailed study of the plumages of the Old-squaw (*Clangula hyemalis*) in which he disagrees with Sutton's conclusions that the species has only two molts and plumages per year. According to Salomonsen, the Old-squaw drake has no less than four plumages: a winter or courtship plumage, breeding or nuptial plumage, eclipse plumage, and autumn plumage. These are rather startling conclusions, but we lack the material to discuss them critically. It remains to be seen whether Salomonsen's interpretation of the plumages of this species are valid. In detail, his findings are as follows:

The winter plumage is worn until April. Around April 10 to 15 the molt into nuptial plumage begins and is completed toward the end of May. This molt affects only head, neck, throat, and the scapulars. The molt into eclipse plumage begins around July 1. There is a period of about three or four weeks in June during which practically no molt takes place. The eclipse molt is completed by the end of August. This molt affects the entire plumage not changed in the previous molt and, according to Salomonsen, also the scapulars. It appears to us that this molt is nothing but a continuation of the April-May molt, even though there may have been some lag during June. It is in this molt that wings and tail are renewed.

A new molt starts in September which affects the feathers of head, neck, throat, flanks, and scapulars. Most of these feathers remain as part of the winter plumage, but the white autumn feathers of the sides of the neck, lores, cheeks, and of the eye and ear region are replaced by the final feathers of the winter plumage.

Although Salomonsen records four molts and four plumages, it follows from his own data that no individual feather papilla has more than one or two molts per year, except the scapulars and some feathers of the head, which, according to him, are molted three times a year. His data also show that there is some scattered molting going on throughout the

year, except from January to March. Thus, actually, Salomonsen's conclusions deviate less from previous descriptions than he implies.

Our knowledge of the molts and plumages of ducks has been notably advanced by Stresemann (1940). His conclusions are based on a series of molting summer ducks from Tibet, where it is apparently easier to get molting pintails and widgeons than in the United States or in Europe! The sequence of molting is different from that described in the current literature. Molt begins with the flank feathers, scapulars and upper tail coverts. Next is the central pair of tail-feathers and the tertials. When the molt of the central pair of tail-feathers is complete, about half the body plumage is in molt, namely, on the upper parts: all the feathers of the crown, many on the sides of head and neck, many of the scapulars, upper tail coverts, and feathers on the middle of the back; on the underparts: nearly all the flank feathers, many feathers of the breast and belly, and many under tail coverts. The last body regions to molt are upper back, rump, upper throat, and chin. In fact, some parts of the rump may never acquire the eclipse plumage. When two to four pairs of tail feathers have molted, the wing is molted. All the wing feathers, wing coverts, and axillaries are molted simultaneously. The tail-feathers molt in the sequence: 1, 2, 4, 6, 7, 3, 5, 8, with some variation in the outer 3 or 4 pairs.

The second half of Stresemann's paper is devoted to a stimulating discussion of the physiological factors that control the plumage. The starting point is the fact that gonadectomized (castrated) adult mallards (male and female) wear the nuptial plumage of the drake throughout the year. This is usually called the "neutral" plumage of the species.

Gonadectomized ducklings, however, retail the normal juvenal plumage (acquiring it again even after plucking), which is for them the neutral plumage. Gonadal hormones obviously produce the eclipse plumage of the male and the "henny" plumage of the immature duck, male and female. Why the juvenal plumage does not react to absence of sex hormones has long been a puzzle. Stresemann suggests that the nuptial plumage of the drake (the "neutral" plumage of the adult) is the mature plumage of the species, and that the maturation process occurs independently of hormones. This same interpretation was advanced some time ago: "All these observations and experiments allow the following interpretation: one of the phenomena of reaching maturity in birds is a gradual change in the structure and pigmentation of the feathers from an immature plumage to a neutral adult dress. This change appears to occur in steps as expressed in the successive molts required to produce the final plumage, but is actually caused by a slow physiological change, as has been proved by plucking feathers between molts. This process is modified by an additional differentiation caused by a female or male hormone, which changes the neutral plumage to a typical female or male adult plumage. This latter process can be reversed by the removal of the gonads, while the change from the im-

mature plumage to the 'Neutral Plumage' seems to be irreversible and independent of any hormones thus far known" (Mayr, 1933:10). Stresemann feels that this interpretation is strengthened by the observation of Heinroth and Lorenz that the eclipse plumage of old drakes is less henny (more nuptial-like) than that of younger drakes. This Stresemann interprets to mean that the older ("more mature") the feather papillae become, the less subject they are to the inhibitory effects of the sex hormones.

An alternative hypothesis would be that it is not the reactivity of the feather papillae which changes, but the level of other endocrine antagonists, such as the hormones of thyroid, pituitary, and the adrenals. Only experiment can tell which of the alternatives is correct—or if the truth is a combination of both processes. Two recent papers throw some light on the problem: Boss (1943) showed that injection of male sex hormone in the chicks of Herring Gulls (*Larus argentatus*) causes them to assume a nuptial plumage in the next molt though they revert to the juvenal plumage as soon as the administration of hormones is discontinued. At least in this species, then, the change from juvenal to adult plumage is not entirely a matter of maturation. Even more significant are the experiments by Chu (1938) on the influence of thyroid hormone on the juvenal plumage of chicks. He shows that thyroidectomized chicks assume a juvenal plumage with the essential characters of the adult neutral plumage. Further work on this question is now being done at the University of Chicago by B. B. Blivaiss and L. V. Domm.

Stresemann's statement that the assumption of the eclipse plumage is not correlated with any special physiological condition of the testes is not convincing. It seems always to be true that the nuptial plumage is acquired during the resting stage of the testes, whereas the eclipse plumage is formed under the influence of an active testis (even though it may be rapidly decreasing in size). A superimposed influence of the thyroid hormone (affecting the growth rate of the new feathers) does not materially change this relationship.

In a final section, Stresemann discusses the manifold correlation between ecology, breeding cycle, and sequence of molts and plumages. It would lead too far to repeat here his many stimulating observations. Every student, either of ducks or of the plumage physiology of birds, should study this pioneer contribution in its entirety.

Lorenz's paper (1941) on the comparative ethology of river ducks has now also reached us. His conclusions on the interrelations of the Anatini are in nearly complete agreement with our conclusions. We hope that it will soon be possible to make this work available to American readers in an English translation, not only for the importance of his conclusions but also as a model of modern ethological technique.

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